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Seasonal variation in diet and prey availability in the wall lizard *Podarcis vaucheri* (Boulenger, 1905) from the Djurdjura Mountains, northern Algeria

Rabah Mamou[a], Faïza Marniche[b], Mansour Amroun[c], Jean-Marie Exbrayat[a] and Anthony Herrel[d]

[a]UMRS 449, General biology - Reproduction and comparative development, Catholic University, EPHE/PSL, Lyon, France; [b]Laboratoire de Zoologie, Veterinary national School, Algiers, Algeria; [c]Laboratoire d'ecologie des Vertébrés, University of Tizi-ouzou, Tizi ouzou, Algeria; [d]Department of Ecology and Biodiversity Management, UMR 7179 C.N.R.S/M.N.H.N., Paris, France

ABSTRACT
We studied the composition and seasonal changes in diet and prey selection in the wall lizard *Podarcis vaucheri* of the Djurdjura Mountains throughout its activity period, from April to October 2014. The analysis of 238 faecal pellets revealed 1 206 prey items distributed in 19 prey categories. The most important prey categories were: Formicidae, Coleoptera, Aranea, Homoptera, and Orthoptera. Significant seasonal variation in the taxonomic composition of the diet and prey availability was found. A significant difference in diet composition was observed between males and females in spring. This lizard species displayed a more diverse dietary spectrum during this period, followed by a slight decrease in summer. However, a severe decrease in the food niche breadth was observed in autumn, resulting in a high consumption of ants. A comparison of diet composition and prey availability showed that lizards exhibited a clear selection of certain prey types, in contrast to what is often suggested for lacertid lizards.

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Dietary spectrum; electivity; food niche breadth; selection; prey types taxonomic composition

Introduction

Dietary studies are central for understanding the evolutionary biology, ecology, and life-history traits of organisms (Pianka and Vitt 2003; Perez-Mellado et al. 2011; Luiselli and Amori 2016). According to Nagy (2005), the most important form of energy for animals is probably that which is contained in the ingested prey. Moreover, the search and acquisition of adequate nutrition is one of the most fundamental challenges that affects the fitness of an animal (Cooper and Vitt 2002).

In the majority of lacertid lizards, terrestrial invertebrates, and particularly insects, make up the predominant part of the diet (Arnold 1987; Carretero 2004; Vitt and Pianka 2007). Previously, lacertid lizards were considered dietary generalists (Arnold 1987) and concomitantly opportunistic predators (Arnold 1987; Mou 1987; Pérez-Mellado and Corti 1993; Lo

CONTACT Rabah Mamou ✉ mamou.rabah@yahoo.fr
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Cascio and Capula 2011). However, some studies have shown that lizards may present an apparent selection of prey (Díaz and Carrascal 1990; Pérez-Mellado et al. 1991; Díaz 1994, 1995; Hódar et al. 1996; Maragou et al. 1996; Adamopoulou and Legakis 2002; Lo Cascio and Capula 2011; Pérez-Cembranos et al. 2016). The diet of this family is characterised by a great variability (Carretero 2004), and prey choice can vary in response to biotic and abiotic factors, such as competition and predation pressure, morphological and physiological constraints, food availability, foraging mode, time of activity, thermoregulatory tactics, and phylogeny (Carretero 2004; Vitt and Pianka 2007).

Podarcis vaucheri (Boulenger, 1905) is a lacertid lizard from the southern Iberian Peninsula and North Africa. This excellent climber mostly prefers bedrock, but also some moisture. It is dependent on rocky, bushy, humid and/or permanent water courses or even forested areas (Schleich et al. 1996; Kaliontzopoulou et al. 2008). It also frequents urbanised areas where it likes sun-exposed walls (Fahd 1993). In the mountains, this lizard lives between plant debris and rocks where soil accumulates (Schleich et al. 1996).

Although formerly considered a subspecies of *Podarcis hispanicus*, it has been elevated to species level (Oliverio et al. 2000; Busack et al. 2005). However, it seems likely that, as in the Iberian Peninsula, various incipient species exist within the *P. vaucheri* complex in North Africa (Lima et al. 2009). Lima et al. (2009) identified four different lineages in Algeria (Moroccan, Tunisian, Aurés and Azazga) and two are exclusively Algerian. This increases the number of "forms" in North Africa to five (Kaliontzopoulou et al. 2011). The Djurdjuran populations belong to the Moroccan line, which is most closely related to the population of the Iberian Peninsula (Lima et al. 2009; Kaliontzopoulou et al. 2011).

Data on the biology and ecology of *P. vaucheri* are scarce, contrary to European *Podarcis* species that are rather well studied. Nevertheless, previous studies have provided data on the trophic ecology (Carretero et al. 2006; Mamou et al. 2016), reproductive biology (Mamou et al. 2017), thermal biology (Veríssimo and Carretero 2009), as well as parasitological studies (Carretero et al. 2011; Damas-Moreira et al. 2014) of this species, allowing us to better understand its biology. In the current paper, we present and discuss the data on the temporal variation in trophic ecology of this species in the Djurdjura Mountains of Algeria. In addition, data on prey availability allow us to better understand diet selection in lacertid lizards in general.

The majority of studies conducted on the feeding ecology of *Podarcis* species were limited to a short period and used small samples and accordingly reflect only part of the trophic strategy of the species studied (Capula et al. 1993; Pérez-Mellado and Corti 1993; Richard and Lapini 1993; Rugiero 1994; Capula and Luiselli 1994; Maragou et al. 1996; Adamopoulou et al. 1999; Bombi et al. 2005; Carretero et al. 2006, 2010; Lo Cascio and Pasta 2006; Kaliontzopoulou et al. 2012; Zuffi and Giannelli 2013; Mamou et al. 2016). Previous ecological studies carried out on *P. vaucheri* diet were limited to a study in spring in the Oukaïmeden Plateau of Morocco (Carretero et al. 2006), or to spring and summer in the same population of this study (Mamou et al. 2016). However, the advantage of the current study was that it provided an overview of the feeding behaviour of *P. vaucheri* during its complete activity cycle, ranging from April to October in the Djurdjura Mountains, in addition to providing data on prey availability throughout the activity season of this lizard.

Materials and methods

Study area

The Djurdjura national park is located in the north east of Algeria in a very rugged mountainous region between Bouira and Tizi-Ouzou. Extending over an area of 18 500 ha, the Djurdjura is the highest of the coastal massifs of Algeria (Lespès 1909). It is characterised by a Mediterranean climate and belongs to the humid bioclimatic stage (Hamdin et al. 1993; Carretero et al. 2011; Amroun et al. 2014). Abundant rainfall is observed during winter (October to May), whereas summers tend to be dry (June to September). According to Krouchi (2010), extrapolations made on the station of Ait-Ouabanes over 20 years, the Tala Guilef station is characterised by an annual thermal amplitude of 23.6 to 25.4 °C and an annual rainfall that can reach 1 652 mm at 1 650 m altitude and 1 852 mm at 1 900 m.

Vegetation is dominated by forests (*Quercus canariensis, Quercus suber, Quercus ilex, Pinus halepensis*, and *Cedrus atlantica*) (Carretero et al. 2011). We conducted our study in the Tala Guilef sector, which is located in the western part of the northern slope of the Djurdjura Mountain. It is located approximately 140 km southeast of Algiers and 45 km southwest of Tizi Ouzou (36°39′ N, 4°01′ E).

The samples were collected in two types of habitat that contained *Podarcis vaucheri*, namely rock formations with various stones and rocks from the Haizer massif, and a river situated between the first rocky habitat and a cedar forest commonly frequented by the lizards during warm hours and/or warm days (see Mamou et al. 2016).

Sampling protocol and diet identification

We captured adult lizards from April to October 2014 by hand or by noose and took them to the laboratory. Faecal pellets were collected by keeping animals in a terrarium (44 cm × 55 cm × 77 cm) heated with a lamp (160 W) placed above one end. Water was provided *ad libitum*. After a day of observation, lizards were released at their site of capture. A total of 238 faecal pellets were obtained (64 in spring, 110 in summer and 64 in autumn), dried and then stored in separate Eppendorf tubes (2 ml) with 70% ethanol and labelled.

Prey items were subsequently identified under a binocular microscope with 10 to 40× magnification, and they were identified down to the lowest possible taxonomic level. However, for a proper analysis of the data, they were separated into Operational Taxonomic Units (OTUs), (Sneath and Sokal 1973; Carretero 2004).

To estimate invertebrates potentially available to *P. vaucheri,* 10 pitfall traps, of 10 cm in diameter and 15 cm in height, were set for 48 hours, between the 13th and 18th of each month. They were placed in line spaced 5 m apart, in the site of capture of the lizards, between the rocky habitat and the river. Afterwards, they were filled with water to a third of their height. The collected material from all traps was preserved in 70% ethanol and was identified to the lowest possible taxonomic level and then classified using the same OTUs as those used for the consumed prey. Note that pitfall traps bias the availability estimates for terrestrial prey and they might accordingly not provide a complete view of the invertebrate prey available to the lizards (Simão et al. 2015).

Data analysis

Diet composition was expressed as: (1) relative occurrence (%P), which is the percentage of pellets containing a prey category (OTU), and (2) relative abundance (%N), which is the percentage of the total number of each category (OTU) in the pellets, (3) trophic niche diversity using the standardised Levin's index (B_A). $B_A = (B - 1)/(n - 1)$, where (n) is the number of OTUs and (B) is the Levin's index of niche breadth: $B = 1/\sum P_i^2$, (P_i) is the proportion of each OTU (i). This index ranges from 0 to 1, where '1' indicates a generalised diet and a value of '0' indicates a specialised diet (Krebs 1999). In addition, we used the Morisita-Horn index (C_H) to estimate similarity between seasonal diets (Horn 1966). $C_H = \frac{2\sum p_{ij}p_{ik}}{\sum p_{ij}^2 + \sum p_{ik}^2}$, where ($P_{ij}$) is the proportion of OTUs (i) in the diet (j) and (P_{ik}) the proportion of OTUs (i) in the diet (k). This parameter varies between 0 (no similarity) and 1 (total similarity) (Krebs 1999).

We used the relativised electivity index (E^*; Vanderploeg and Scavia 1979) to characterise prey selection.

$$W_i = (R_i/P_i)/\sum(R_i/P_i)$$

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

W_i is the selectivity coefficient of OTU (i), (R_i) is the proportion of OTU in the diet, (P_i) is the proportion OUT (i) in the environment, and finally (n) is the number of OTUs. The values of (E^*) ranges between '−1' (avoidance) and '1' (selection). It is important to note that a positive electivity index (E^*) indicates that a particular prey category was eaten more relative to its availability, but not that the lizards prefer these prey items in the sense of showing a behavioural preference for that prey. Only OTUs present in both the faeces and traps were considered in for electivity indices (Carne and Measey 2013). The estimation of the E^* dispersion (standard error and 95% confidence limits) was obtained by 1 000 bootstrap replicates in R.

In addition, two categories (OTUs) were eliminated: Orthoptera, because our sampling method reflects essentially terrestrial prey and flying prey were poorly represented in our samples, and Collembola, which were never eaten by lizards, despite their availability, because of their small size.

Regarding season and sex, the data were tested for normality using the Shapiro–Wilk test; afterwards we used the Kruskal–Wallis *H*-test and Mann–Whitney *U*-tests to compare the number of items per faeces and the Chi-square test of independence (χ^2) to compare the relative frequencies of the OTUs. We also used a Spearman rank correlation (r_s) to examine the relation between relative abundance (%N) and relative occurrence (%P) of prey categories and to estimate, firstly, the relationship between diet and prey availability. Statistical analyses were performed using the XLSTAT-Pro software, version 7.1 (ADDINSOFT 2004). The bootstrap simulation and the principal component analysis were done using the "boot" and "ade4" packages, respectively, under the R-environment, version 3.4.3 (R Core Team 2017).

Results

Taxonomic composition of the diet

The food spectrum of *P. vaucheri* was composed mainly of arthropods (Table 1). The analysis of 238 faecal pellets revealed 1 206 items grouped into 19 OTUs, representing 5.07 items/faeces. With respect to relative abundance (%N), insects were the most represented with 87.29% of ingested prey followed by spiders (10.84%). For the categories Opiliones, Arachnida, Acari, Gastropoda, and plants, the relative abundance (%N) did not exceed 1%.

According to the relative abundance and occurrence values, we found that among insects, four categories (OTUs) were highly consumed: Formicidae, Coleoptera, Hemiptera and finally Orthoptera. There was a significant positive rank correlation between relative abundance (%N) and relative occurrence (%P) of prey OTUs ($r_s = 0.97$, $p < 0.0001$). Indicating that frequently eaten prey were also consumed in large quantities.

Several genera and species of Formicidae were identified and three families of beetles were most commonly consumed: Staphylinidae (27.74%) and Scarabaeidae (24.52%), followed by Curculionidae (12.26%). Regarding the Homoptera, the family of Cicadellidae dominated with 82.09% and for Orthoptera Acrididae were most often found (83.19%).

No significant difference in the mean number of items per faeces was observed between the two sexes (Mann–Whitney *U*-test: $Z = 0.29$, $p = 0.77$). Also, throughout the period of activity of *P. vaucheri*, males and females showed a similar diet composition ($\chi^2 = 8.45$, $DF = 18$, $p = 0.97$). Indeed, there was no difference between males and females in summer ($\chi^2 = 14.72$, $DF = 17$, $p = 0.616$) and autumn ($\chi^2 = 13.91$, $DF = 12$, $p = 0.306$). However, a significant difference was observed in spring ($\chi^2 = 24.33$, $DF = 12$, $p = 0.018$), with males consuming mainly Coleoptera, Araneae and Diptera and females consuming Araneae, Coleoptera and Hymenoptera.

Dietary variation

The mean number of items per faeces (mean ± SE) varied from 4.1 ± 0.32 in spring to 4.7 ± 0.39 in summer, with a slight increase in autumn to 6.7 ± 1.11. However, there was no significant difference between the three seasons (Kruskal–Wallis *H*-test: $H = 1.54$, $p = 0.46$). The highest value was attributed to a faeces sampled in September, composed of 57 items, of which 55 came from a single ant species, *Solenopsis* sp.

A statistical analysis showed a significant influence of seasonal variation on the diet of *P. vaucheri* in Djurdjura ($\chi^2 = 74.12$, $DF = 17$, $p < 0.0001$). Figure 1 shows a detailed overview of this variation. In spring, the diet was more diversified ($B_A = 0.45$) and 13 OTUs were identified. The most consumed were: Coleoptera, Araneae and Diptera. In summer, we observed a change in the diet composition and a light reduction in food niche diversity ($B_A = 0.36$). Among the 18 OTUs consumed, the most represented were: Homoptera, Formicidae, Orthoptera, and Araneae. During autumn, there was a dramatic reduction in the trophic niche breadth ($B_A = 0.08$) and a large part of the diet consisted of winged ants, which become gregarious to reproduce during this period.

The largest similarity was noted between two successive seasons, and the highest value of the Morisita–Horn index (C_A) assigned to spring–summer (0.49), followed by summer–autumn (0.45). The lowest value was attributed to spring–autumn (0.27).

Table 1. Taxonomical composition of the diet in *Podarcis vaucheri* and prey categories (OTUs) in the field. %P: occurrence; %N: relative abundance; *n*: number of identified items; and B_A: standardised Levin's index.

	Spring					Summer					Autumn						
	Diet				Available	Diet				Available	Diet				Available		
	Males		Females			Males		Females			Males		Females			Total diet	
OTUs	%N	%P	%N	%P	%N	%N	%P	%N	%P	%N	%N	%P	%N	%P	%N	%N	%P
Acari	0	0	0	0	0	0	0	1.08	2.38	0	0.67	4.76	0	0	0	0.21	0.84
Arachnida	0	0	0	0	6.42	0	0	0.54	2.38	1.47	0	0	0	0	8.79	0.06	0.42
Araneae	13.56	45	22.35	70.83	5.07	13.29	32.35	8.11	33.33	3.43	5.33	33.33	4.65	33.33	1.83	10.84	37.82
Archeognatha	0	0	0	0	0	0	0	0	0	0.49	0	0	0	0	0	0	0
Chilopoda	0	0	0	0	0.68	0	0	0	0	0	0	0	0	0	0.18	0	0
Coleoptera	38.42	67.5	18.82	41.67	17.91	6.65	25	4.32	14.29	6.24	2.67	14.29	3.49	25	15.75	15.82	35.71
Collembola	0	0	0	0	23.31	0	0	0	0	4.65	0	0	0	0	14.29	0	0
Dermaptera	0.56	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0.21	0.84
Dictyoptera	2.26	10	0	0	0.34	1.81	7.35	6.49	19.05	3.79	1.33	9.52	0	0	0.55	2.22	9.66
Diplopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.37	0	0
Diptera	12.43	40	5.88	16.67	4.73	6.04	19.12	5.41	23.81	3.43	1.33	9.52	1.16	8.33	4.95	5.84	20.59
Formicidae	5.08	17.5	5.88	20.83	17.23	16.92	27.94	16.22	40.48	65.48	78.67	61.9	84.88	91.67	45.6	29.84	36.97
Gastropoda	0	0	0	0	0	0.91	2.94	1.62	7.14	0	0	0	0	0	0	0.39	2.10
Hemiptera	3.39	12.5	7.06	20.83	0	0.6	1.47	1.08	4.76	0	0.67	4.76	3.49	25	0	2.25	7.98
Heteroptera	3.95	10	5.88	16.67	3.04	0.91	4.41	4.86	16.67	0.24	0	0	0	0	0	2.61	8.82
Homoptera	2.82	7.5	0	0	12.84	23.87	45.59	23.24	42.86	2.2	0.67	4.76	2.33	16.67	0.18	9.06	24.79
Hymenoptera	6.78	20	16.47	29.17	3.04	3.02	10.29	8.11	21.43	1.59	2.67	19.05	0	0	1.28	6.40	19.33
Isoptera	0	0	0	0	0.34	0.3	1.47	0.54	2.38	1.96	0	0	0	0	0	0.13	0.84
Lepidoptera larvae	4.52	17.5	7.06	25	0.68	0	0	0.54	2.38	0.37	0.67	4.76	0	0	0.73	2.08	7.14
Neuroptera	0	0	0	0		6.65	8.82	3.24	7.14	0	0	0	0	0	0	1.81	3.78
Opiliones	0.56	2.5	1.18	4.17	2.36	0.30	1.47	0	0	1.59	0.67	4.76	0	0	5.31	0.86	2.94
Orthoptera	5.65	22.5	9.41	25	0.68	18.43	67.65	13.51	45.24	0.49	4	28.57	0	0	0	9.01	39.92
Pseucoptera	0	0	0	0	1.01	0	0	0	0	0	0	0	0	0	0	0	0
Thysanoptera	0	0	0	0	0.34	0	0	0	0	0.12	0	0	0	0	0.18	0	0
Vegetal matter	0	0	0	0	0	0.3	0	1.08	2.38	0	0.67	4.76	0	0	0	0.35	1.26
Number of pellets	40		24			68		42			21		43				
items/pellet Mean ± SE	4.42 ± 0.40		3.54 ± 0.54			4.87 ± 0.57		4.40 ± 0.42			7.14 ± 2.01		6.46 ± 1.35			5.07 ± 0.36	
Number of items	262					516					428					1 206	
B_A	0.42				0.63	0.36				0.08	0.08				0.23		

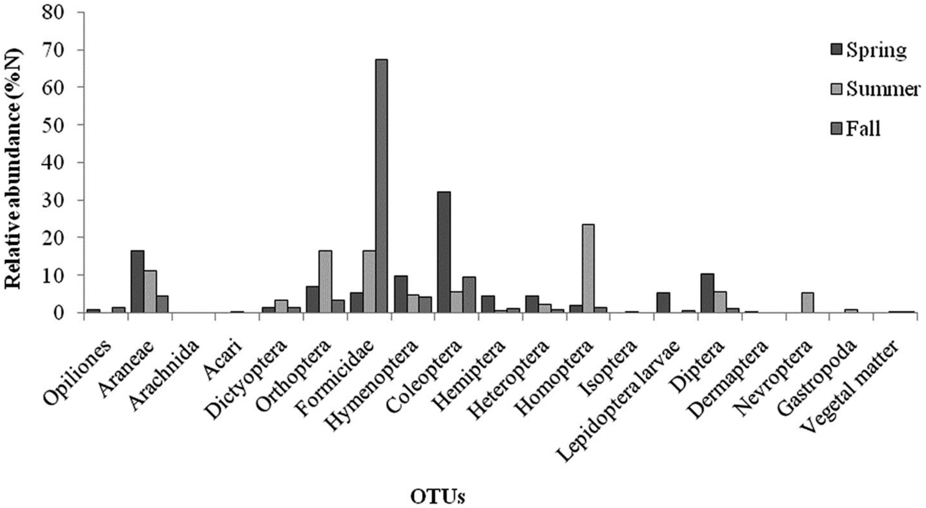

Figure 1. Seasonal variation among the different OTUs in the diet of *Podarcis vaucheri*.

Prey availability and electivity

Statistical analysis revealed significant seasonal variation in the invertebrate community ($\chi^2 = 29.757$, DF = 18, $p = 0.040$). An examination of table one shows that the invertebrate community appears more diversified in spring ($B_A = 0.63$) with the dominant prey being: Collembola (23.31%), Coleoptera (17.91%), Formicidae (17.23%) and Homoptera (12.84%). In summer, we noticed a reduction in prey availability ($B_A = 0.08$), and only Formicidae dominated (65.48%). However, in autumn, we observed an increase in available prey diversity ($B_A = 0.23$), but ants remained the most abundant: Formicidae (45.6%), Coleoptera (15.75%) and Collembola (14.29%).

During the three study seasons there was no correlation between prey consumed by females and prey availability (spring: $r_s = 0.299$, $p = 0.321$; summer: $r_s = 0.492$, $p = 0.053$; autumn: $r_s = 0.492$, $p = 0.104$), but in the case of males diet, we detected a significant correlation with prey availability in spring ($r_s = 0.612$, $p = 0.026$) and summer ($r_s = 0.508$, $p = 0.045$) and no correlation in autumn ($r_s = 0.188$, $p = 0.559$). However, the Vanderploeg and Scavia relativised electivity indices (E^*) ranged between −0.953 and 0.741 (Table 2), and the comparison between the categories (OTUs) showed a significant difference (one-way ANOVA: $F_{12} = 5.04$, $p < 0.0001$).

The bootstrap simulation showed a marked change in the selection of prey during the three seasons considered (Figure 2). However, we limited our analysis to the five most consumed OTUs: Formicidae, Coleoptera, Homoptera, Araneae and Diptera. In spring, *P. vaucheri* had a neutral selection for beetles, but strongly avoided these in summer and autumn. Ants were avoided in spring and summer, but a neutral selection was noted in autumn. Homoptera were rejected in spring, yet selected in summer and autumn. However, the electivity of lizards for spiders varied only a little and remained close to zero throughout the lizards' activity cycle. Diptera, were consumed in spring and summer, yet were avoided in autumn.

Table 2. Potential available prey and prey consumed by *Podarcis vaucheri*. A: available OTUs, E: eaten OTUs, *E** = Electivity index with standard error (SE) and confidence interval (CI 95%) after 1 000 bootstraps.

OTUs	Spring				Summer				Autumn			
	A	E	*E** ± SE	CI 95%	A	E	*E** ± SE	CI 95%	A	E	*E** ± SE	CI 95%
Arachnida	19	0			12	1	−0.637 ± 0.469	(−0.951, −0.037)	48	0		
Araneae	15	43	0.117 ± 0.448	(−0.826, 0.623)	28	59	−0.168 ± 0.469	(−0.606, 0.720)	10	20	0.059 ± 0.431	(−0.748, 0.651)
Coleoptera	53	84	−0.1722 ± 0.438	(−0.903, 0.494)	51	30	−0.487 ± 0.469	(−0.936, 0.528)	86	41	−0.585 ± 0.430	(−0.876, 0.144)
Dictyoptera	1	4	0.326 ± 0.458	(0.002, 0.695)	31	18	−0.517 ± 0.450	(−0.947, 0.399)	3	7	0.160 ± 0.423	(−0.565, 0.718)
Diptera	14	27	−0.073 ± 0.456	(−0.892, 0.493)	28	30	−0.062 ± 0.462	(−0.814, 0.678)	27	6	−0.781 ± 0.421	(−0.988, −0.148)
Formicidae	51	14	−0.783 ± 0.442	(−0.93, −0.136)	535	86	−0.751 ± 0.454	(−0.958, −0.541)	249	289	−0.221 ± 0.427	(−0.839, 0.499)
Heteroptera	9	12	−0.247 ± 0.455	(−0.923, 0.345)	2	12	0.497 ± 0.451	(0.350, 0.710)	0	4		
Homoptera	38	5	−0.889 ± 0.441	(−0.928, −0.887)	18	122	0.585 ± 0.470	(0.547, 0.742)	1	7	0.551 ± 0.438	(0.554, 0.637)
Hymenoptera	9	26	0.130 ± 0.447	(−0.758, 0.674)	13	25	−0.108 ± 0.458	(−0.636, 0.723)	7	19	0.187 ± 0.423	(−0.489, 0.706)
Isoptera	1	0			16	2	−0.487 ± 0.461	(−0.936, 0.515)	0	0		
Lepidoptera	2	14	0.498 ± 0.445	(0.491, 0.674)	3	1	−0.589 ± 0.465	(−0.950, 0.288)	4	3	−0.397 ± 0.438	(−0.857, 0.454)
Opiliones	7	2	−0.768 ± 0.453	(−0.933, −0.055)	13	1	−0.917 ± 0.461	(−0.953, −0.916)	29	7	−0.769 ± 0.424	(−0.879, −0.721)

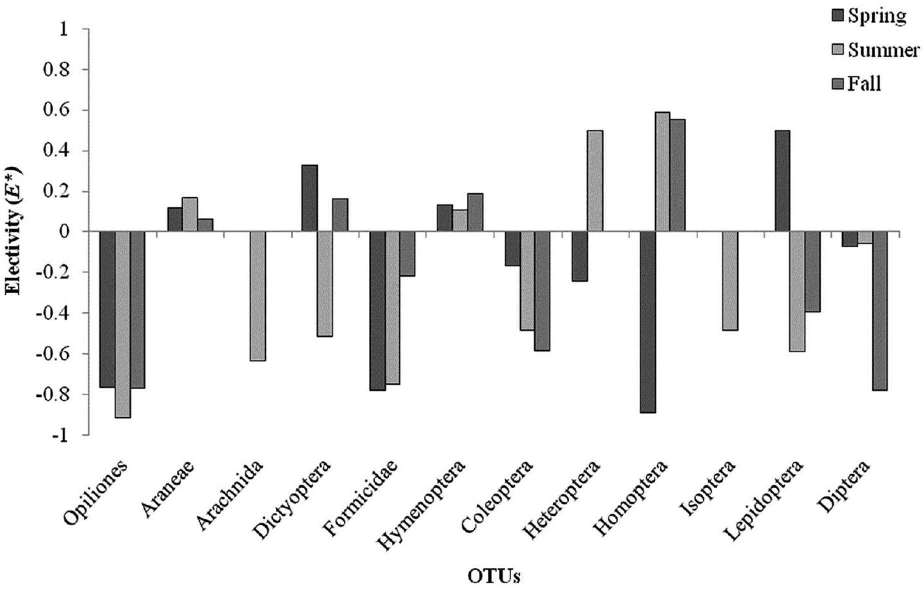

Figure 2. Seasonal variation of the electivity index (*E**).

Discussion

Our results indicate that *P. vaucheri* has a primarily arthropod-based diet, composed principally of insects, as reported for other *Podarcis* species (Mou 1987; Capula et al. 1993; Pérez-Mellado and Corti 1993; Richard and Lapini 1993; Rugiero 1994; Capula and Luiselli 1994; Vicente et al. 1995; Maragou et al. 1996; Adamopoulou et al. 1999; Adamopoulou and Legakis 2002; Burke and Mercurio 2002; Bombi et al. 2005; Carretero et al. 2006, 2010; Lo Cascio and Pasta 2006; Lo Cascio and Capula 2011; Kaliontzopoulou *et al.* 2012; Zuffi and Giannelli 2013; Mamou et al. 2016; Pérez-Cembranos et al. 2016).

However, the series of studies conducted on the diet of *Podarcis* species revealed particular adaptations to trophic resource scarcity. This was notably observed in the case of herbivory and myrmecophagy, commonly observed in several populations from the Mediterranean islands (Ouboter 1981; Pérez-Mellado and Corti 1993; Adamopoulou et al. 1999; Van Damme 1999; Adamopoulou and Legakis 2002; Bombi et al. 2005; Herrel et al. 2008; Carretero et al. 2010; Brock et al. 2014; Pérez-Cembranos et al. 2016). However, extreme trends in the feeding ecology in this genus were recorded, including the consumption of marine prey (Castilla et al. 2008, 2009), oophagy (Brock et al. 2014; Žagar et al. 2016), the consumption of conspecifics (Pérez-Mellado and Corti 1993; Rugiero 1994; Castilla and van Damme 1996; Pafilis et al. 2009; Capula and Aloise 2011; Grano et al. 2011; Žagar and Carretero 2012; Simović and Marković 2013; Pérez-Cembranos et al. 2016), other lizard species or small mammals (Capula and Aloise 2011; Dias et al. 2016), as well as scavenging (Pérez-Cembranos et al. 2016). As reported by Herrel et al. 2008 and Vervust et al. 2010 in *Podarcis siculus*, these adaptations to island conditions, mainly herbivory, can induce rapid microevolutionary changes in morphology.

The diet of *P. vaucheri* is characterised by a great number of food categories (OTUs) ingested and a clear seasonality in its food spectrum and feeding strategy. Furthermore, the comparison of the diet composition revealed an absence of correlation with prey availability. However, the electivity index calculated for each period showed that lizards seemed to avoid some prey and selected others, depending on the environmental conditions and requirements of the lizards. Moreover, this selective predation has already been reported in other species of Lacertidae (Díaz and Carrascal 1990; Pérez-Mellado et al. 1991; Díaz 1994, 1995; Hódar et al. 1996; Maragou et al. 1996; Adamopoulou and Legakis 2002; Lo Cascio and Capula 2011; Pérez-Cembranos et al. 2016).

The analysis of trophic diversity indicates that *P. vaucheri* has a more diversified diet in spring. Limited to this period, our results are in agreement with those reported by Carretero et al. 2006 and Mamou et al. 2016, and revealed a similar diet to that known in the *Podarcis* genus, with a preference for beetles, as reported in many studies (Maragou et al. 1996; Adamopoulou et al. 1999; Carretero et al. 2006; Lo Cascio and Capula 2011; Mamou et al. 2016; Vicente et al. 1995; Maragou et al. 1996; Zuffi and Giannelli 2013). Furthermore, an avoidance of other prey categories, such as ants and Homoptera, was also observed in spring.

During summer, there was a decrease in diet diversity, partly, owing to the reduction in prey availability, but probably also to the reduction of the time available for activity, because of the high temperatures observed in summer. This is illustrated by our availability results, where summer showed the lowest diversity in invertebrate availability. However, given that our analysis was based on pitfall traps only, these results might be biased if a high abundance of flying insects are present in summer. However, visual observations did not suggest an exceptional abundance of flying insects at the sampling site. Despite high availability of ants in the environment during this period, they are not eaten by lizards, which consumed Homoptera, as reported for *P. muralis* (Mou 1987; Richard and Lapini 1993), followed by the Orthoptera, ants and spiders. However, the high consumption of these prey, particularly Homoptera, Orthoptera, Araneae, is possibly related to their high water content, allowing lizards to compensate for the lack of water in summer, as reported in other Lacertidae (Pollo and Perez-Mellado 1988; Adamopoulou and Legakis 2002; Mamou et al. 2016).

An interesting finding was the high consumption of ants in autumn, followed by a strong reduction in food niche breadth (Figure 3). Lizards also became less selective in autumn associated with an increase in available prey diversity. Feeding on ants has been documented for both mainland and insular species of *Podarcis* (Pérez-Mellado and Corti 1993; Capula and Luiselli 1994; Carretero 2004; Bombi et al. 2005). This can be explained by the gregarious nature of ants; which became a profitable food source during this period. This strategy might allow a predator to reduce the energy used in search for food, and therefore might compensate for their weak profitability and noxiousness of these prey (Pollo and Perez-Mellado 1988, 1991; Pérez-Mellado and Corti 1993; Carretero 2004; Mella et al. 2010). This is reminiscent of an “optimal foraging” approach, defined as the difference between energetic contribution of prey and the energy expended by a predator to catch and ingest it, relative to the time required to capture a prey (Schoener 1971; Stamps et al. 1981). In addition, there was an increase in the average number of items per faeces during this period. This strategy might be used by lizards to rebuild the reserves and compensate the energetic resources expended

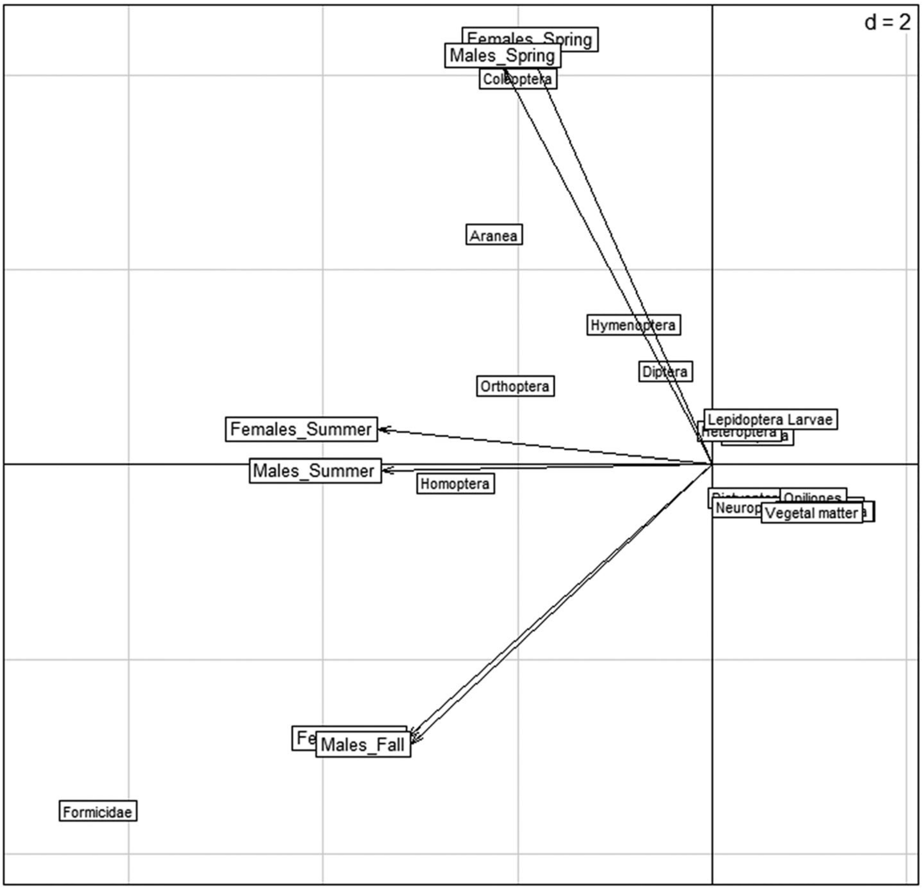

Figure 3. Plot score from the principal component analysis describing the dietary trends of *Podarcis vaucheri*

during breeding period, before approach of the winter and the entry into hibernation (Vicente et al. 1995; Carretero 2004).

The overall diet of *P. vaucheri* suggests that males and females share a common pattern in their feeding ecology; except in spring, when reproductive interactions forced both sexes to shift their dietary preferences, allowing a reduction of competition between them. However, in summer and autumn, both sexes are likely obliged to converge in their diets, as a result of a lack of available resources. Also, regarding correlation of diet with prey availability during breeding season, our results suggest that males might have a different optimization strategy, probably exploiting larger timeslots compared with the females.

Concerning the type of prey in diet, *P. vaucheri* consumed mainly terrestrial prey like Coleoptera, spiders, Hymenoptera, Homoptera, Heteroptera and Orthoptera. These types of prey are suggestive of active foraging, as reported by Carretero et al. (2006) and Mamou et al. (2016), and typical of most Mediterranean lacertids.

Although the data can improve the knowledge of trophic ecology in *P. vaucheri*, our estimation of food availability might be limited. We only used pitfall traps; therefore, flying insects were underrepresented in our sample. Also, the traps were active at night and they might have trapped nocturnal arthropods that are not readily available to lizards, because of their diurnal activity pattern.

In conclusion, the diet of *P. vaucheri* was characterised by strong seasonal variations**,** attributed to variation in insect availability, changes in activity, as a result of temperature differences between seasons, difference in trophic requirements related to reproductive status and the approach of the cold season and hibernation. However, it would be interesting to test the influence of morphological parameters, such as head size and shape on the choice of prey (e.g. Herrel et al. 1996; Verwaijen et al. 2002; Huyghe et al. 2007; Kaliontzopoulou et al. 2012; Sagonas et al. 2014).

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References

Adamopoulou C, Legakis A. 2002. Diet of a Lacertid lizard (*Podarcis milensis*) in an insular dune ecosystem. Isr J Zool. 48(3):207–219.

Adamopoulou C, Valakos ED, Pafilis P. 1999. Summer diet of *Podarcis milensis, P. gaigeae* and *P. erhardii* (Sauria: Lacertidae). Bonn. Zool. Beit. 48:275–282.

ADDINSOFT. 2004. Xlstat for Excel, version 7. 5. New York, USA: Addinsoft.

Amroun M, Bensidhoum M, Delattre P, Gaubert P. 2014. Feeding habits of the common genet (*Genetta genetta*) in the area of Djurdjura, north of Algeria. Mammalia. 78(1):35–43.

Arnold EN. 1987. Resource partition among lacertid lizards in southern Europe. J Zool (Lond). 1 (4):739–782.

Bombi P, Vignoli L, Scalera R, Bologna MA. 2005. Food habits of *Podarcis filfolensis* (Reptilia, Lacertidae) on a small Mediterranean island during the dry season. Amphib-Reptil. 26(3):412–417.

Brock MK, Donihue MC, Pafilis P. 2014. New records of frugivory and ovophagy in *Podarcis* (Lacertidae) lizards from East Mediterranean Islands. North-West J Zool. 10:223–225.

Burke RL, Mercurio RJ. 2002. Food habits of a New York population of Italian wall lizards, *Podarcis sicula* (Reptilia, Lacertidae). Am Midl Nat. 147(2):368–375.

Busack SD, Lawson R, Arjo WM. 2005. Mitochondrial DNA, allozymes, morphology and historical biogeography in the *Podarcis vaucheri* (Lacertidae) species complex. Amphib-Reptil. 26(2):239–256

Capula M, Aloise G. 2011. Extreme feeding behaviours in the Italian wall lizard, *Podarcis siculus*. Acta Herpetol. 6:11–14.

Capula M, Luiselli L. 1994. Resource partitioning in a Mediterranean lizard community. Bolletino Zool. 61(2):173–177.

Carne L, Measey GJ. 2013. Chameleons on the cruise: seasonal differences in prey choice of two dwarf chameleons. Herpetol J. 23:221–227.

Carretero MA. 2004. From set menu to a la carte. Linking issues in trophic ecology of Mediterranean lacertids. Ital J Zool (Modena). 71sup2:121–133.

Carretero MA, Cascio PL, Corti C, Pasta S. 2010. Sharing resources in a tiny Mediterranean island? Comparative diets of *Chalcides ocellatus* and *Podarcis filfolensis* in Lampione. Bonn Zool. Bull. 57:111–118.

Carretero MA, Perera A, Harris DJ, Batista V, Pinho C. 2006. Spring diet and trophic partitioning in an alpine lizard community from Morocco. Afr Zool. 41(1):113–122.

Carretero MA, Roca V, Larbes S, Ferrero A, Jorge F. 2011. Intestinal helminth parasites of wall lizards, *Podarcis vaucheri* complex (Sauria: Lacertidae) from Algeria. J Herpetol. 45(3):385–388.

Castilla AM, Herrel A, Gosa A. 2009. Marine prey in the diet of *Podarcis atrata* from the Columbretes Islands. Munibe. 57:187–190.

Castilla AM, Vanhooydonck B, Catenazzi A. 2008. Feeding behaviour of the Columbretes lizard *Podarcis atrata*, in relation to Isopoda (Crustaceae) species: *ligia italica* and *Armadillo officinalis.* Belg J Zool. 138:146–148.

Cooper WE Jr, Vitt LJ. 2002. Distribution, extent, and evolution of plant consumption by lizards. J Zool (Lond). 257(4):487–517.

Damas-Moreira I, Harris DJ, Rosado D, Tavares I, Maia JP, Salvi D, Perera A. 2014. Consequences of haemogregarine infection on the escape distance in the lacertid lizard, *Podarcis vaucheri*. Acta Herpetol. 9:119–123.

Díaz JA. 1994. Effects of body temperature on the predatory behavior of the lizard *Psammodromus algirus* hunting winged and wingless prey. Herpetol J. 4:145–150.

Díaz JA. Prey selection by lacertid lizards: a short review. Herpetol J. 1995. 5:245–251.

Díaz JA, Carrascal LM. 1990. Prey Size and Food Selection of *Psammodromus algirus* (Lacertidae) in Central Spain. J Herpetol. 24(4):342–347.

Fahd S. 1993. Atlas préliminaire des reptiles du Rif (Nord du Maroc). Thèse troisième cycle, Abdelmalek Essaâdi, Tétouan, Maroc. 166 p.

Grano M, Cattaneo C, Cattaneo A. 2011. A case of cannibalism in *Podarcis siculus campestris* De Betta, 1857 (Reptilia, Lacertidae). Biodivers J. 2(3):151–152.

Hamdine WH, Thevenot M, Sellami M, De Smet K. 1993. Régime alimentaire de la Genette (*Genetta genetta* Linné, 1758) dans le Parc national du Djurdjura, Algérie. Mammalia. 57:9–18.

Herrel A, Van Damme R, De Vree F. 1996. Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. Neth J Zool. 46(3):253–262.

Herrel A, Huyghe K, Vanhooydonck B, Backeljau T, Breugelmans K, Grbac I, Van Damme R, Irschick DJ. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proc Natl Acad Sci USA. 105(12):4792–4795.

Hódar JA, Campos F, Rosales BA. 1996. Trophic ecology of the ocellated lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey. J Arid Environ. 33(1):95–107.

Huyghe K, Vanhooydonck B, Herrel A, Tadic Z, Van Damme R. 2007. Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis.* Integr Comp Biol. 47(2):211–220.

Kaliontzopoulou A, Adams DC, Van Der Meijden A, Perera A, Carretero MA. 2012. Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. Evol Ecol. 26(4):825–845.

Kaliontzopoulou A, Pinho C, Harris DJ, Carretero MA. 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. Biol J Linn Soc Lond. 103(4):779–800.

Kaliontzopoulou A, Brito J, Carretero MA, Larbes S, Harris DJ. 2008. Modelling the partially unknown distribution of wall lizards *Podarcis* in North Africa: ecological affinities, potential areas of occurrence and methodological constraints. Can J Zool. 86(9):992–1101.

Krouchi F. 2010. Etude de la diversité de l'organisation reproductive et de la structure génétique du cèdre de l'Atlas (*Cedrus atlanticus* Manetti) en peuplement naturel (Tala Guilef, Djurdjura nord-ouest, Algérie). [PhD thesis]. Mouloud Mammeri University, Tizi Ouzou, Algeria.

Lespes R. 1909. Le climat de la Kabylie du Djurdjura. Ann Geogr. 18(97):24–33.

Lima A, Pinho C, Larbes S, Carretero MA, Brito JC, Harris DJ. 2009. Relationships of *Podarcis* wall lizards from Algeria based on mtDNA data. Amphib-Reptil. 30(4):483–492.

Lo Cascio P, Capula M. 2011. Does diet in lacertid lizards reflect prey availability? Evidence for selective predation in the Aeolian wall lizard, *Podarcis raffonei* (Mertens, 1952) (Reptilia, Lacertidae). Biodivers J. 2:89–96.

Lo Cascio P, Pasta S. 2006. Preliminary data on the biometry and the diet of a microinsular population of *Podarcis wagleriana* (Reptilia: lacertidae). Acta Herpetol. 1:147–152.

Luiselli L, Amori G. Diet. 2016. In: Kenneth Dodd C, editor. Reptile Ecology and Conservation: A Handbook of Techniques. Oxford: Oxford University Press. p. 97–109.

Mamou R, Marniche F, Amroun M, Herrel A. 2016. Trophic ecology of two sympatric lizard species: the Algerian sand lizard and the wall lizard in Djurdjura, northern Algeria. Zool Ecol. 26(4):256–264.

Mamou R, Moudilou E, Amroun M, Exbrayat J-M. 2017. Reproductive cycle of male wall lizard, *Podarcis vaucheri* (Reptilia: Sauria: Lacertidae), in Djurdjura. Northern Algeria. Basic Appl Herpetol. 31:77–89.

Maragou P, Valakos ED, Giannopoulos Z, Stauropoulou A, Chondropoulos BP. 1996. Feeding ecology of *Podarcis peloponnesiaca* (Sauria: Lacertidae) in spring. Herpetozoa (Wien). 9:105–110.

Mella J, Tirado C, Cortés A, Carretero MA. 2010. Seasonal variation of prey consumption by *Liolaemus barbarae*, a highland lizard endemic to Northern Chile. Anim Biol Leiden Neth. 60(4):413–421.

Mou Y. 1987. Ecologie trophique d'une population de lézards des murailles *Podarcis muralis* dans l'ouest de la France. Rev Ecol. 42:81–100. [Terre Vie].

Nagy KA. 2005. Field metabolic rate and body size. J Exp Biol. 208(Pt 9):1621–1625.

Oliverio M, Bologna MA, Mariottini P. Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Teira* Gray, 1838 (Reptilia, Lacertidae). J Biogeogr. 2000;27(6):1403–1420.

Ouboter PE. 1981. The ecology of the island-lizard *Podarcis sicula salfii.* Amphib-Reptil. 2(3):243–257.

Pafilis P, Meiri S, Foufopoulos J, Valakos E. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften. 96(9):1107–1113.

Pérez-Cembranos A, León A, Pérez-Mellado V. 2016. Omnivory of an insular lizard: sources of variation in the diet of *Podarcis lilfordi* (Squamata, Lacertidae). PLoS One. 11(2):e0148947.

Pérez-Mellado V, Bauwens D, Gil M, Guerrero F, Lizana M, Ciudad M-J. 1991. Diet composition and prey selection in the lizard *Lacerta monticola.* Can J Zool. 69(7):1728–1735.

Pérez-Mellado V, Corti C. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: sauria). Bonn Zool Beitr. 44:193–220.

Perez-Mellado V, Pérez-Cembranos A, Garrido M, Luiselli L, Corti C. 2011. Using faecal samples in lizard dietary studies. Amphib-Reptil. 32(1):1–7.

Pianka ER, Vitt LJ. 2003. Lizards: Windows to the Evolution. California: University of California Press.

Pollo CJ, Perez-Mellado V. 1988. Trophic ecology of a taxocenosis of mediterranean Lacertidae. Ecol Mediter. 14:131–147.

Pollo CM, Pérez-Mellado V. 1991. An analysis of a Mediterranean assemblage of three small lacertid lizards in Central Spain. Acta Oecol. 12:655–671.

Richard, J., L. Lapini. 1993. Trophic niche overlap in syntopic populations of *Lacerta horvathi* and *Podarcis muralis* (Reptilia, Lacertidae). Atti Mus. civ. St. nat. 45:151–157.

Rugiero L. 1994. Food habits of the ruin lizard, *Podarcis sicula* (Rafinesque-Schmaltz, 1810), from a coastal dune in Central Italy. Herpetozoa (Wien). 7:71–73.

Sagonas K, Pafilis P, Lymberakis P, Donihue CM, Herrel A, Valakos ED. 2014. Insularity affects head morphology, bite force and diet in a Mediterranean lizard. Biol J Linn Soc Lond. 112(3):469–484.

Schleich HH, Kästle W, Kabisch K. 1996. Amphibians and Reptiles of North Africa: Biology, Systematics, Field Guide. Koenigstein: Koeltz Scientific Books.

Schoener TW. 1971. Theory of feeding strategies. Annu Rev Ecol Syst. 2(1):369–404.

Simão FCP, Carretero MA, Amaral MJA, Do, Soares AMV. 2015. Composition and seasonal variation of epigeic arthropods in field margins of NW Portugal. Turk J Zool. 39:404–411.

Simović A, Marković A. 2013. A case of cannibalism in the common wall lizard, *Podarcis muralis*, in Serbia. Hyla. 2013:40–41.

Sneath PHA, Sokal RR. 1973. Numerical Taxonomy. CA. San Francisco, New York: Freeman.

Stamps J, Tanaka S, Krishnan VV. 1981. The relationship between selectivity and food abundance in a juvenile lizard. Ecology. 62(4):1079–1092.

Van Damme R. 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. J Herpetol. 33(4):663.

Vanderploeg HA, Scavia D. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol Modell. 7(2):135–149.

Veríssimo CV, Carretero MA. 2009. Preferred temperatures of *Podarcis vaucheri* from Morocco: intraspecific variation and interspecific comparisons. Amphib-Reptil. 30(1):17–23.

Vervust B, Pafilis P, Valakos ED, Van Damme R. 2010. Anatomical and physiological changes associated with a recent dietary shift in the lizard *Podarcis sicula.* Physiol Biochem Zool. 83(4):632–642.

Verwaijen D, Van Damme R, Herrel A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. Funct Ecol. 16(6):842–850.

Vicente LA, Araujo PR, Barbault R. 1995. Écologie trophique de *Podarcis bocagei berlengensis* et de *Lacerta lepida* (Sauria, Lacertidae) sur l'île de Berlenga (Portugal). Rev Ecol. 50:317–351. [Terre Vie].

Vitt LJ, Pianka ER. 2007. Feeding ecology in the natural world. In: Reilly SM, Mcbrayer LD, Miles DB, editors. Lizard Ecology. United Kingdom: Cambridge University Press. p. 141–172.

Žagar A, Carretero MA. 2012. A record of cannibalism in *Podarcis muralis* (Laurenti, 1768) (Reptilia, Lacertidae) from Slovenia. Herpetol Notes. 5:211–213.

Zuffi MA, Giannelli C. 2013. Trophic niche and feeding biology of the Italian wall lizard, *Podarcis siculus campestris* (De Betta, 1857) along western Mediterranean coast. Acta Herpetol. 8:35–39.